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Stimulation of a sensory receptor initiates a nervous message, which, on arrival in the brain, undergoes modification; and may produce, in the mind, a related sensory experience. Some recent investigations on the vertebrate visual system have shed some light on the peripheral coding and central analysis of this kind of sensory message.

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"SOME ASPECTS OF FUNCTIONAL ORGANISATION IN THE CEREBRAL CORTEX"

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Stimulation of a sensory receptor initiates a nervous message, which, on arrival in the brain, undergoes modification; and may produce, in the mind, a related sensory experience. Some recent investigations on the vertebrate visual system have shed some light on the peripheral coding and central analysis of this kind of sensory message.

Some of the earliest investigations on the nature of the retinal message were made by Adrian and Matthews in 1927 and 1928, using eyes excised from conger eels. On recording action potentials from the whole nerve, they found that, in complete darkness, the nerve was almost wholly inactive; but illumination produced a discharge of high frequency impulses. These declined in frequency, on continued illumination, to a steady low level of activity, which lasted for the whole period of the illumination. On turning off the light, they noted a slight diminution of frequency (lasting for about 1/10 second), followed by a short-lived high frequency burst, and then complete cessation of activity. The latency of these responses, and their maximum spike frequency, were related to the quantity of light falling on the receptors in unit time; but this only held for retinal areas less than 1 mm in diameter, and was not effective with areas greater than this. Movement of a light, or shadow, was a more effective stimulus than a steady object. This then, was an "on" and "off" activity.

The activity of individual optic nerve fibres, and, therefore, of individual ganglion cells, was first analysed by Hartline in 1938. Using the bullfrog's eye he exposed the fundus by removing cornea, lens and choroid, and dissected out single optic nerve fibres from the small bundles on the retinal surface. By this extremely difficult technique, he found that not all the fibres responded to the same stimulus. They seemed to fall into 3 main categories, which he named "on", "off", and "on-off". This diversity of the response was independent of the local physical conditions of stimulation (i.e. Temperature, pH, anoxia, etc.) and was probably, therefore, an inherent property of the ganglion cells.

The "on" type of cell (comprising 20% of the total investigated) responded when a light was on, and maintained its discharge as long as the illumination continued. Those that responded with a burst of impulses when the light was switched on, and again when it was switched off, but fell silent during continued illumination, were called "On-Off" cells (50% of total); while those that gave a short burst only on the "Off" of illumination, were called "Off" cells (30% of total). These categories were not rigid, however, and occasional

intermediate types were seen. The receptive field of each ganglion cell was about 0.5 — 1.0 mm. in diameter.

Some "On-Off" cells had a central plateau of greater sensitivity (its diameter varying between 0.2 and 0.6 mm). Light outside this area had to be about 1,000 - 10,000 times brighter to achieve the same response, and could *inhibit* the response which would have occurred if that part had not also been illuminated. This seemed to indicate an inhibitory surround to the receptive fields of the cells.

Although the essential character of the responses remained unchanged, the duration of exposure to "illumination" did affect the strength of the response: i.e. the strength of the "Off" response depended on the time of exposure to the preceding light—the strength of the "On" response on the time of exposure to the preceding dark; while the "on-off" cells showed a combination of both. Re-illumination of the retina could suppress the "off" discharge and a strong response to small movements could be elicited in the "on-off" cells. Barlow, in 1953, using a Micro-electrode technique of recording from single fibres on the intra-optic (retinal) surface of the exised frog's eye preparation, confirmed most of these findings.

Also in 1953, Kuffler investigated the organisation of the receptive fields of single fibres in the mammalian optic nerve. By inserting micro-electrodes through the intact eyeball of a cat he could record from single units on the retinal surface. He found, contrary to Adrian and Matthews in the eel, that, in the dark adapted cat there was spontaneous activity in the absence of illumination. (A micro electrode placed in the centre of the optic disc recorded a mass spontaneous discharge, which could be suppressed by dim illumination of the whole retina.) With a small exploring spot of light and background illumination, he confirmed, for cats, that all units had a central area of greater sensitivity, with either "off" activity, or "on", predominating. For example, in the "on-centre" type, when the spot was shifted towards the periphery of the receptive field, the "on" activity decreased and "off" activity appeared. With the spot even further in its periphery, a zone of pure "off" activity could be detected. This arrangement was reversed in units with an "off-centre". Illumination of both areas together produced little or no activity. Thus each receptive field had a mutually antagonistic centre-surround arrangement.

The role that this type of receptive field organisation played in the analysis of visual patterns in the frog, was investigated in 1959 and 1960 by an American team. This group, Maturana, Lettvin, McCulloch, and Pitts, used a series of stimuli which they thought might be significant to the frog in catching prey—small dark discs a few degrees in diameter, broad and narrow dark strips, small squares, etc. These could be used, moving or stationary, against a series of different backgrounds. Using these visual stimuli, and recording single units by Micro-electrode penetration of the optic nerve, they found that the ganglion cells had five different functional classes—one recording light intensity, and the other four each giving a maximal response to one quality, or configuration of qualities, in the visual stimulus. Each ganglion cell responded only to one type of configuration and any departure from this gave a reduction in, or disappearance of, the response. With the exception of the class that indicated light intensity, they seemed to be independent of the general illumination, the nature of the background, and the state of dark adaptation of the eye. The receptive fields for each of these 5 classes appeared to be uniformly distributed over the retina.

The first class called "sustained-edge detectors", responded to a sharp edge, either darker or lighter than the background, moved through the receptive

field of the cell. The response was largely independent of the shape of the object, or its curvature; but there seemed to be an optimal size, speed and position, for a maximal response. The activity could be suppressed by a switch to complete darkness, but was restored on restoration of the illumination. This group of receptors were equated with Hartline's "on" group. The second group were called "convex-edge detectors", and gave a maximal response to movement of a very small object 1.5 in diameter. They gave no response to straight edges, but were sensitive to corners, and tended to respond only to movements towards the centre of the receptive field. A light object on a dark background gave a poor response—unless it had a dark shadow. These two classes of ganglion cell were not entirely separable, and a small number were found to give an intermediate response. Thus the two classes may have represented the two peaks of a bimodal distribution, so that different cells might respond maximally to slightly different stimulus parameters (i.e. each may have a different optimal object size etc.).

The third class were sensitive to the "on" and "off" of light, and to movements in any direction in the receptive field. These "changing-contrast detectors", equivalent to Hartline's "on-off" grouping, gave no activity with a stationary contrast, but *did* respond—although poorly—to movements of a banded or complex background. The fourth class "dimming detectors", responded to the "off" of light, or to a moving object (irrespective of its size or shape) in proportion to the dimming it produced. These were thus equivalent to Hartline's "off" receptors; but changing conditions were essential for the responses, continued darkness soon ended the activity. The last class were the "dark detectors". These were found to be continuously active even in light, but their activity was inversely proportional to the light intensity, giving a maximal response in the dark. The retinal distribution seemed to be uniform for each type of ganglion cell receptive field, although the total numbers of each class differed considerably.

Similar results were obtained by recording from single units in the optic tectum of the frog (units thought to be the terminals of the ganglion cell axons).

Hubel and Wiesel, in a paper published in January, 1962, demonstrated the existence, in the cat's visual cortex, of a system of organisation not unlike that in the frog. However, in the cat, these cells, which likewise responded to one invariable in the visual stimulus, seem to be of true cortical origin. In a previous paper (1959), they had shown by using a small light-spot stimulus, and recording by micro-electrodes from single units in the cat's striate cortex, that the receptive fields of these cells were divided into mutually antagonistic excitatory and inhibitory regions. These were not necessarily circular, or even symmetrical, and their arrangement determined the required stimulus size, shape and orientation for maximal response. In 1962, they again recorded from single units in the cat's striate cortex, but this time used a series of different stimulus shapes on a tangent screen background. With these, they found that the receptive fields of these cortical cells could be divided into two functional classes, "simple" and "complex" according to the type of visual stimulus needed to activate them.

The responses of the "simple" cells could be predicted by exploring the receptive field with a small light-spot. These had receptive fields divided into antagonistic, excitatory and inhibitory zones; and thus movement of an object out of an inhibitory, and into an excitatory zone would be a very effective stimulus. However the orientation of the stimulus was critical, as not all the

receptive fields had similarly arranged excitatory and inhibitory zones, for example—a narrow central zone with two antagonistic flanks, symmetrical or asymmetrical; large central zones and small antagonistic flanks; and those with one excitatory and one inhibitory region. Here the most effective stimulus would be an "edge" moving one way only—from the inhibitory to the excitatory zone).

The "complex" cells had responses not predictable by mapping the receptive fields with small light-spots, which, if effective at all, gave just a mixture of "on-off" regions. They were of four main types, each activated by a different combination of stimulus parameters. The first type required a horizontal slit of highly specific size (1.8° wide 3° long), but the exact position of this slit in the receptive field was not critical, as long as it remained horizontal. An upward movement of the stimulus produced a discharge, a downward movement suppressed it, and if the slit was stopped, there was no discharge. The second type was also activated by a slit of similar dimensions, but oriented 10 o'clock - 4 o'clock. Movements either up or down stimulated it, but stopping it stopped the discharge, as did changing the orientation. The third type responded to an edge, vertically oriented, either with excitation or inhibition depending on whether the area of brightness was to the left or to the right, but again its position in the receptive field was immaterial. The fourth type only responded to a dark bar on a light screen, not the converse. In the example studied, the orientation was critical (horizontal), and it was sensitive to downward movements only—giving a weak, inconsistent response to upward movement, and none at all to movements left and right. Except for the injured ones, all the simple and complex units that they recorded, showed some sort of response to a visual stimulus; but their receptive fields showed great variation in size (although the complex ones tended to be larger).

By recording from cells in sequence during one micro-electrode penetration, they found that successive cells tended to have identical axis orientation. But changes of angle did occur, and these were unpredictable. The cell types tended to be layered according, roughly, to the cortical layers, i.e. "simple" cells were confined mainly to layers 3, 4 and 6, while "complex" cells were extremely rare in layer 4. Although the receptive fields were of different size, there was at least a gross topographical point-to-point representation of the retina preserved down through the columns, with, as usual in the visual system, a correspondingly large area devoted to the area centralis of the retina. This topographical representation seems to be an essential prerequisite of functional organisation in the vertebrate visual system, and has been seen at most levels (e.g. tectum or superior colliculus, lateral geniculate nucleus, and cortex) in most species (refs. 7-11). The magnification of the central area is likewise a common feature and may be related to the number of ganglion cells devoted to the central area (Jacobson, 1962).

It can, therefore, be seen from this type of experiment, that the mosaic of active and inactive receptors (rods and cones) must be of a rather specific pattern to activate a retinal ganglion cell in the frog. But, in the cat, the ganglion cells are activated by a less complex pattern of receptors (Kuffler's centre-surround arrangement), while the cortical cells require a more complex receptor organisation. Hubel and Wiesel have suggested a tentative scheme for the possible interconnections of just such a system. In this several centre-surround ganglion cells connected in a specific way will determine the stimulus requirements of a "simple" cortical cell, and several of the "simple" type will determine those of a "complex" cell. Although only a few

preliminary experiments have been conducted on the primate visual cortex (monkey), these would seem to indicate that a similar arrangement—of cells with simple and complex receptive fields, grouped into discrete columns and preserving the point-to-point topography—may well exist, but large differences are likely.

The process whereby the geometrical arrangement of inter-connections between groups of neurones can serve to abstract, for a particular animal, the significant parameters from a mass of sensory data, and the central vertico-topographical segregation of these parameters, may well be a general principle of functional organisation in the vertebrate nervous system. Some work done by Mountcastle in 1957, on the somatic sensory cortex in monkeys, indicates a similar columnar organisation of incoming sensory data. But here, the sensory modality (e.g. touch, pain, pressure, etc.) seems to be the functional grouping used. Topographic representation of the body surface is likewise preserved. And Penfield, in his 1958 Sherrington Lectures, cites the case of a patient E.C., who had experiential hallucinations just before a major epileptic convulsion. In these, he (E.C.), always relived a childhood experience where he had snatched a stick from the mouth of a dog. Any subsequent experience where he saw "someone snatching something from someone" served to trigger off another attack; and electrical stimulation of the temporal cortical lobes did the same. Penfield suggests that this "snatching" no matter in what aspect, may result in a neurone impulse reaching the neurone pattern that records previous "snatching" experience, and that this might be thought of as a "*biological cross-indexing of abstract characteristics of experiences so that each fresh example has its immediate connection with (similar) previous experiences*".

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